The neurocognitive basis of knowledge about object identity and events: Dissociations reflect opposing effects of semantic coherence and control

Elizabeth Jefferies[1], Hannah Thompson[2], Piers Cornelissen[3] and Jonathan Smallwood[1]

1. University of York, UK
2. University of Surrey, UK
3. Northumbria University, UK

Correspondence to: Beth Jefferies, Department of Psychology, University of York, UK, beth.jefferies@york.ac.uk

Abstract

Semantic memory encompasses knowledge of specific objects and their diverse associations, but the mechanisms that allow us to retrieve aspects of knowledge required for a given task are poorly understood. The Dual Hub theory suggests that separate semantic stores represent knowledge of (i) taxonomic categories (in the anterior temporal lobes, ATL) and (ii) thematic associations (in angular gyrus, AG or posterior middle temporal gyrus, pMTG). Alternatively, the Controlled Semantic Cognition (CSC) framework suggests that semantic processing emerges from the flexible interaction of heteromodal semantic representations in ATL with a semantic control network, which includes pMTG as well as prefrontal regions. According to this view, ATL supports patterns of coherent auto-associative retrieval, while semantic control sites respond when ongoing conceptual activation needs to be altered to suit the task or context. These theories make different predictions about the nature of functional dissociations within the semantic network. We review evidence for these claims across multiple methods. First, we show ATL is sensitive to the strength of thematic associations as well as taxonomic relations. Next, we document functional dissociations between AG and pMTG: rather than these regions acting as comparable thematic hubs, AG is allied to the default mode network and supports more 'automatic' retrieval, while pMTG responds when control demands are high. However, the semantic control network, including pMTG, also shows a greater response to events/actions and verbs, supporting the claims of *both* theories. We propose that tasks tapping event semantics often require greater shaping of conceptual retrieval than comparison tasks, since these elements of our knowledge are inherently flexible, with relevant features depending on the context. In this way, the CSC account might be able to account for findings that suggest both a process and a content distinction within the semantic network.

A current challenge in cognitive neuroscience is to explain how the brain produces diverse patterns of semantic retrieval for the same concept in different contexts [1, 2] – for example, we understand that CAR is associated with TRAFFIC JAM when it occurs together with HOLIDAY, but also with RACING when we encounter it with TRACK. This capacity for flexible retrieval is shared across words and objects [3, 4] and is critical to our comprehension of events, since the concept CAR takes on different properties in these circumstances [e.g. slow moving vs. fast moving; 2, 5]. Recent theoretical accounts of semantic cognition propose that flexible semantic cognition emerges from the interaction of multiple neurocognitive components, but there is controversy about the functional organisation of these components [1, 6-8]. Diverse features (for example, visual, auditory, motor, praxis, valence, linguistic) are thought to be integrated within 'semantic hub' regions to create heteromodal concepts [e.g., 1, 8, 9], yet there remains controversy about the number and nature of these hubs [8, 10, 11]. In addition, conceptual representations are thought to interact with control processes in order to focus ongoing retrieval on currently-relevant aspects of knowledge [12-15], but the nature of this interaction – and how it generates task- and context-appropriate patterns of retrieval – is poorly understood.

Two alternative theoretical accounts

Contemporary theories of semantic cognition explain conceptual flexibility in different ways (see Figure 1). Multiple accounts assume that heteromodal conceptual processing is supported by 'hub' regions which integrate different types of features which are, to varying degrees, grounded in sensory-motor experience [1, 8, 10]. Distinct hubs might capture different combinations of features, relevant to the representation of different kinds of conceptual information, reflecting their patterns of connectivity [e.g., 16] and/or they might support distinct processes required to acquire or retrieve particular aspects of knowledge [e.g., 6]. The *Dual Hub* account suggests that there are different heteromodal hub regions that store taxonomic vs. thematic information [11]. The anterior temporal lobes (ATL) are thought to underpin taxonomic knowledge about objects and their features, while temporoparietal regions such as angular gyrus (AG) and/or posterior middle temporal gyrus (pMTG) support knowledge of thematic associations and events. This theory was originally put forward to explain different types of picture naming errors in patients with aphasia, following damage to different cortical regions. Co-ordinate semantic errors, such as ZEBRA → HORSE, occur commonly in patients with ATL lesions, while thematic associative errors, such as ZEBRA → ZOO, are associated with temporoparietal lesions affecting AG and pMTG. Schwartz and colleagues [11] suggested this pattern of picture naming errors might arise if damage to distinct semantic hubs gives rise to noisy responses

within conceptual representations that capture different kinds of semantic relations. While the Dual Hub account did not directly address the issue of semantic flexibility, we might imagine that different patterns of retrieval suitable for (i) identifying and categorising specific objects and (ii) understanding events and thematic associations could emerge through the interaction of these taxonomic and thematic hubs with control processes. During categorisation or other tasks requiring access to taxonomic knowledge, control regions such as left inferior frontal gyrus (IFG) might prioritise activity in ATL, while in a thematic association-matching task, IFG might prioritise activity in temporoparietal hubs such as AG/pMTG; however, this idea remains largely untested.

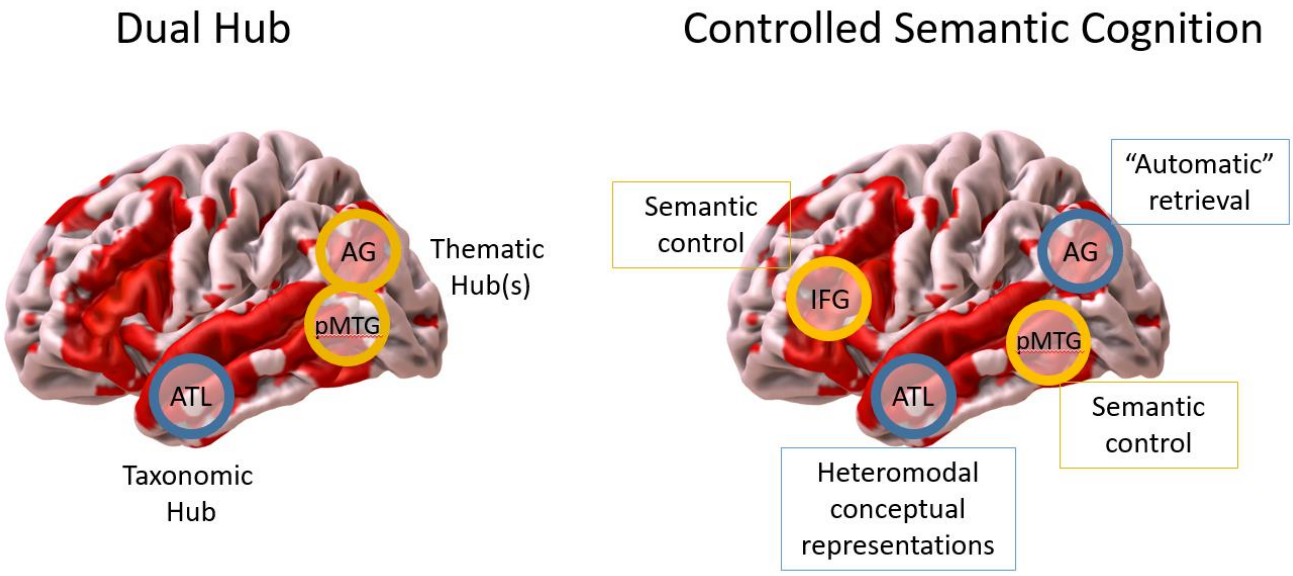

Figure 1: A schematic depiction of alternative theories of semantic components. The regions shown in red are implicated in semantic processing by a meta-analysis in Neurosynth [17] using the term "semantic". The Dual Hub account suggests a role for temporoparietal cortex – including AG and/or pMTG – in representing thematic knowledge, as opposed to taxonomic knowledge in ATL. The Controlled Semantic Cognition framework alternatively proposes that ATL represents both taxonomic and thematic relations, and that pMTG works in concert with other regions such as IFG to support semantic control processes. ATL = anterior temporal lobes. pMTG = posterior middle temporal gyrus. AG = angular gyrus. IFG = inferior frontal gyrus.

In contrast to the Dual Hub account, the Controlled Semantic Cognition (CSC) framework proposes that different aspects of knowledge are captured within a single semantic hub within the ventral ATL [1, 9]. Different patterns of coupling of the hub with sensorimotor 'spokes' can then support the

retrieval required for specific tasks [18, 19]. Within word-picture matching, identifying animals is thought to involve stronger interaction between vATL and visual features, while identifying tools involves greater recruitment of motor features [20, 21]. Knowledge of thematic associations might involve greater involvement of language or action systems than knowledge of objects, since we talk about and/or use associated items together [6, 22].

Nevertheless, differential recruitment of the spokes is not sufficient to explain the full flexibility of semantic cognition. This is because we have acquired many features and associations for any given concept, some of which are dominant within the long-term conceptual store (e.g., SALT-PEPPER), and some of which are not (e.g., SALT-ICY). Within this theoretical framework, control processes are thought to help us shape patterns of semantic retrieval to suit the task. For example, if we need to understand the link between RACING CAR and a weakly-associated item, such as CHAMPAGNE, control processes might inhibit dominant associations of these concepts (e.g., TRACK and GRAPES), to selectively focus on the circumstances in which these items co-occur (e.g., on the PODIUM). Similarly, if we want to identify the taxonomic overlap between two items from the same category that rarely co-occur and which share few features (e.g., MEERKAT and CLOWN FISH), control processes may be needed to direct retrieval away from dominant yet irrelevant features for each concept (e.g., STANDS ERECT; ORANGE) and towards overlapping yet weakly-encoded features (MOVES; HAS EYES). Semantic regions that maintain currently-relevant aspects of knowledge in a form of working memory or conceptual context, distinct from long-term semantic similarity in ATL, could be one way of achieving this flexibility in retrieval. The CSC framework proposes that these semantic control regions include both left IFG and pMTG.

In this review article, we discuss the evidence for the contradictory claims made by the Dual Hub and CSC models. The predictions made by these two theoretical frameworks are summarised in Figure 1 and Table 1. First, we consider the role of ATL in semantic cognition. We review the evidence that this site specifically supports taxonomic knowledge, and find evidence across multiple methods that computations within ATL are also relevant to the comprehension of thematic associations. Next, we consider evidence that pMTG and/or AG form a 'thematic hub'. While the Dual Hub account proposes a dissociation between AG/pMTG (thematic hub) and ATL (taxonomic hub), the CSC framework instead suggests a dissociation between ATL (representational hub) and pMTG/IFG (implicated in semantic control). We show that the functional profile of these regions, and their patterns of intrinsic connectivity, support the second of these views. Finally, we propose an account of the functional contributions of key semantic sites which is largely compatible with the empirical evidence offered in support of the dual hub and CSC theories. To anticipate, we suggest that ATL and pMTG support qualitatively different semantic processes (coherent retrieval vs. contextually-guided

control). This may give rise to differential recruitment of these regions during taxonomic and thematic judgements, as well as accounting for the greater engagement of pMTG in controlled semantic cognition, if these tasks typically tap these processes to different degrees.

Table 1: Predicted response profiles in ATL and left pMTG made by different theoretical accounts

	ATL	pMTG
Dual Hub	Stronger responses to taxonomic than thematic relations	Stronger responses to thematic than taxonomic relations
Controlled Semantic Cognition	Equivalent response to different types of semantic relations	Stronger response when semantic control demands are high across different types of semantic relations

Does ATL provide a taxonomic hub?

Proponents of the Dual Hub theory have suggested that ATL is a taxonomic hub, which represents object identity [6, 11]. This view is consistent with the observation that ATL lies at the end of the ventral visual stream; a neural pathway which supports the transformation of visual perception to conceptual representation [e.g., 23]. This view explains why ATL plays a critical role in identifying objects and representing their physical features [9]. Its cortical location is suitable for learning about patterns of overlapping physical features, potentially underpinning our knowledge of taxonomic categories (at least for concrete concepts).

However, research suggests that the contribution of ATL to semantic cognition extends beyond taxonomic judgements and the identification of objects. These observations are consistent with the CSC account, which proposes that ATL supports the representation of thematic as well as taxonomic relations [1]. Much of our knowledge of the role of the ATL in cognition has come from the study of patients with semantic dementia (SD), who have progressive yet relatively focal atrophy and hypometabolism within ventral ATL [9, 24]. SD patients have difficulty across a wide range of semantic tasks – and show correlations across tests that involve identifying concepts and retrieving thematic associations, suggesting they have degradation of a central semantic store recruited across tasks [25]. Although patients with SD have relatively focal neurodegeneration in ATL, the atrophy and hypometabolism becomes more extensive within temporal and inferior frontal cortex as the condition progresses. For this reason, it is important that converging evidence from healthy

participants has confirmed a role of ATL in both taxonomic and thematic decisions. Focal inhibitory transcranial magnetic stimulation (TMS) to ATL disrupts both types of tasks in healthy participants [26, 27], while fMRI studies of healthy volunteers show that both taxonomic and thematic judgements recruit this brain region [28].

One difficulty in interpreting these results is that the successful identification of associations necessarily requires initial identification of the concepts presented in the task: therefore, it is hard to discount the possibility that impairment or activation of ATL in thematic decisions reflects a role for this structure in identifying individual concepts. This problem is overcome to some extent by studies that demonstrate that ATL is sensitive to the *strength* of thematic associations. Patients with SD show strong effects of frequency, both in their knowledge of concepts and their thematic associations [29]. Concepts that are encountered relatively frequently are better preserved in these patients – less familiar concepts such as CAMEL become degraded at an earlier stage of the disease than highly familiar concepts such as HORSE [30]. A similar pattern is also seen in thematic association tasks – knowledge of strong associations (RACING CAR-TRACK) is better preserved than knowledge of weaker associations (RACING CAR-CHAMPAGNE; Jefferies & Lambon Ralph, 2006). These effects might occur because information about concepts and their associations that has been encountered more times in the past is represented more robustly in ATL, because strong thematic associations and high-frequency concepts tend to be acquired at an earlier age [31], and because the semantic system continues to learn even as it degrades [32, 33] – and high-frequency associations as well as concepts continue to be experienced during this process. To conclude, these results show that conceptual processing in ATL is sensitive to the strength of thematic associations. Although it remains possible that SD gives rise to disproportionate degradation of knowledge of physical features [cf. 34], it is unlikely that computations within ATL are irrelevant to thematic associations.

A similar sensitivity in ATL to the strength of thematic relations is seen in neuroimaging studies of healthy participants. ATL (together with AG) shows effects of "combinatorial semantics"; these sites show a stronger response to sets of concepts that combine together in meaningful ways [35-37]. For example, they show more activation to longer fragments of language that allow an overarching meaning to be computed over multiple items [38]. In recent work combining MEG and chronometric TMS, we examined the neural response in ATL to pairs of thematically-linked words that were strongly or weakly-associated [39]. The first word in the pair was the same across conditions, and we examined the neural response to the second item. ATL showed a larger difference from a baseline period for strong than weak associations and TMS to this site also disrupted the efficient retrieval of strong associations to a greater extent (even though these trials were easier). In a follow-up study using MEG [40], we compared the neural response in ATL for taxonomic and thematic decisions

(matched for difficulty) and for strong and weak thematic associations (varying in difficulty). The response in ATL was greater for words that were more strongly related – and this pattern was observed irrespective of the type of decision (e.g. taxonomic/thematic). The taxonomic trials elicited a stronger response than the weak thematic decisions in ATL, even though these conditions were matched on behavioural performance – and this might have reflected the greater semantic overlap for the taxonomic items, as measured by word2vec (which measures whether items are used in similar linguistic contexts). We also observed a stronger response in ATL for strongly- as opposed to weakly-associated thematic trials, replicating the results of Teige et al. (2018). Taken together, these findings are consistent with the view that ATL responds more to sequences of inputs in which there is conceptual coherence between the items – irrespective of whether this semantic similarity reflects (i) overlapping physical features in taxonomic trials or (ii) dominant thematic relations. Differences in task difficulty and differential deactivation across conditions do not appear to account for our MEG and TMS findings.

This sensitivity of ATL (and, in some studies, AG) to semantic similarity is consistent with the view that these sites provide an integrative semantic 'hub'. If ATL computes heteromodal conceptual representations from the combination of different types of inputs (within the spokes), a stronger response might be expected for successive items that have strongly overlapping features or associations (as in the experiments above). As a real-world example, when you hear BARKING, in an expected location such as a KENNEL, you might activate the visual features of DOG more strongly than when one of these elements occurs alone – and this might elicit a stronger response in ATL [cf. 41]. These findings taken together are consistent with the proposal that ATL shows auto-associative properties, giving rise to pattern completion effects in semantic retrieval. This is likely to be largely sufficient for semantic cognition when the task or context requires dominant or highly accessible semantic information (given long-term learning and/or recent experience). In other circumstances, when non-dominant or less easily accessed aspects of knowledge are required, the CSC framework proposes that retrieval is shaped by semantic control processes, to bring currently-relevant features and associations to the fore (see below). Consequently, the CSC proposal suggests that neural recruitment underpinning coherent, relatively uncontrolled semantic retrieval will be largely focused within anterior aspects of the temporal lobe, as opposed to semantic control structures in pMTG/IFG, irrespective of whether the task probes knowledge of object identity, taxonomic relationships, specific physical features or thematic associations.

Do temporoparietal regions provide a thematic hub?

The Dual Hub and CSC frameworks also make different claims about the functional contribution of temporoparietal regions – pMTG and AG – to semantic cognition. While the Dual Hub account focuses on the role of one or both of these regions in thematic representation, the CSC framework proposes that pMTG supports semantic control. Evidence in line with the Dual Hub account is provided by patients with left temporoparietal lesions, who show reduced incidental activation of thematic relations during comprehension [42] as well as a tendency to make thematic errors in picture naming tasks (e.g., ZEBRA → ZOO), following damage to the putative thematic hub [11]. Left temporoparietal (and prefrontal) lesions are also associated with ideational apraxia, characterised by difficulty using objects in a meaningful way, especially in the context of complex multi-step actions like making a cup of tea: patients produce errors such as selecting coffee instead of tea, or adding sugar twice. These patients with temporoparietal lesions have difficulty understanding actions in meaningful contexts and their problems with action semantics correlate with thematic matching deficits [43, 44]. These difficulties are consistent with the Dual Hub proposal that temporoparietal cortex represents knowledge of event structures. However, patients tend to have large lesions encompassing both AG and pMTG. Therefore, it is difficult to establish from neuropsychological evidence alone the extent to which each of these regions individually shows the characteristics of a thematic hub.

Strong converging evidence for the role of pMTG in the comprehension of actions and events across modalities is provided by fMRI and TMS studies of healthy participants. For example, Wurm and Caramazza [45] used multi-voxel pattern analysis of fMRI data to show that pMTG represents actions in a similar way across observed scenes and written descriptions. This site also activates in response to action understanding [5, 46, 47], tool recognition [48] and to verbs more than nouns [49-53]. Causal evidence for a role of pMTG in verb processing is provided by inhibitory TMS [54]. Interestingly, the role of pMTG in verb processing cannot be entirely explained in terms of its role in understanding actions: pMTG supports the processing of both action and non-action verbs [49, 50, 55]. These observations suggest that pMTG might support event structures or aspects of contextually-guided semantic retrieval, which are important even for non-motoric verbs. It remains unclear whether this contribution reflects heteromodal long-term representations of action/event/thematic knowledge in pMTG (as envisaged by the Dual Hub view), or instead processes that are particularly important for understanding events. For example, the CSC framework suggests pMTG is critical for semantic control, which might be more heavily taxed by event > object contrasts in prior studies [5]. In line with this viewpoint, patients with semantic control deficits show

ideational apraxia, irrespective of whether they have lesions in left temporoparietal or inferior prefrontal cortex [4, 56, 57].

pMTG and AG fall within different large-scale networks

In the original formulation of the Dual Hub account [11], there was uncertainty about the exact location of the thematic hub within temporoparietal cortex: both AG and pMTG were implicated. While some fMRI studies have observed activation of both AG and pMTG for the contrast of thematic > taxonomic judgements [58], more recent evidence suggests these brain regions have different functional profiles and patterns of intrinsic connectivity (see Figure 2). Left pMTG is implicated in a large-scale distributed semantic control network (along with other regions, such as left IFG). In contrast, left AG shows a stronger response to patterns of semantic retrieval that are tightly constrained or undemanding, and it forms part of the default mode network (DMN), which typically deactivates during demanding tasks [59]. This functional distinction within temporoparietal cortex is highlighted through the comparison of two activation likelihood meta-analyses. One meta-analysis by Noonan et al. [60] identified common activation across diverse manipulations of semantic control demands, including the contrast of weak vs. strong thematic associations, ambiguous vs. non-ambiguous words and strong vs. weaker distractors. Left pMTG along with IFG, and pre-supplementary motor cortex, were found to respond in all of these contrasts (see Figure 2). The opposite pattern was found for left AG in a meta-analysis by Humphreys & Lambon Ralph [61]: this site responded to 'automatic' semantic tasks without significant control demands (e.g. strong > weak associations), as well as to the retrieval of episodic and numerical facts from long-term memory.

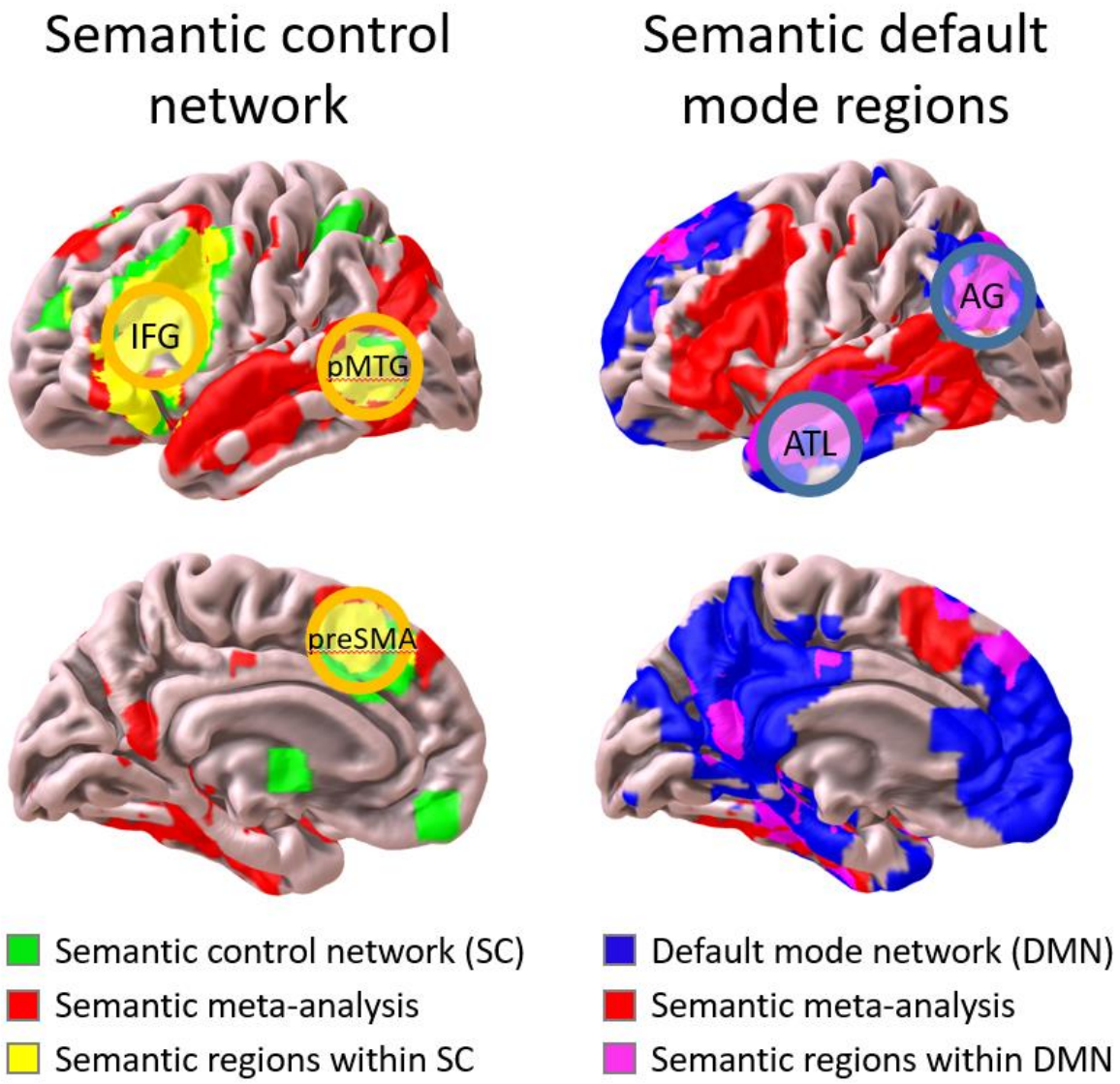

Figure 2: Semantic meta-analysis (in red) is derived from Neurosynth [17]. The semantic control map (in green/yellow) is a meta-analysis of studies that manipulated the control demands of semantic tasks in diverse ways, from Noonan et al. [60]. The default mode network map is taken from Yeo et al. [62]. ATL = anterior temporal lobes. pMTG = posterior middle temporal gyrus. AG = angular gyrus. IFG = inferior frontal gyrus. preSMA = pre-supplementary motor area.

In line with the CSC framework, convergent evidence across multiple methods shows that left pMTG forms a functional network for semantic control along with left IFG. First, lesions centred on either left IFG or pMTG in the context of semantic aphasia (SA) are associated with disordered semantic retrieval [63, 64], suggesting these sites play a critical role in semantic control. Although patients with SA and SD fail the same range of semantic tasks – including tests of object identification,

thematic matching and synonym judgement – they show a qualitatively different pattern of semantic impairment [30, 64]. Individuals with SD are highly consistent in the concepts they can understand across different tasks (suggesting degradation of central concepts), while SA patients are more sensitive to the context in which conceptual information must be processed [4, 64]. SA patients show stronger effects of cues and miscues, implying that their conceptual knowledge is relatively intact and their impairment reflects difficulty internally constraining their retrieval to suit the circumstances [63, 65]. SA patients also show increasing difficulty accessing concepts when a small set of semantically-related items are repeatedly probed in cyclical tasks – irrespective of whether these sets are related taxonomically or thematically – and strong effects of distractor strength [66-68]. Many of these characteristics map onto an earlier distinction first drawn by Warrington and colleagues between semantic storage and access deficits: as in SA, patients with semantic access deficits are insensitive to item frequency/familiarity, show less consistency in the knowledge they can retrieve, and demonstrate 'refractory' effects when semantically-related items are probed in quick succession [69, for a review, see 70].

Over multiple studies, we have demonstrated that patients with SA have heteromodal semantic deficits that vary with the control demands of semantic tasks. They have impaired comprehension of the subordinate associations of ambiguous words (e.g., BANK refers to RIVER not MONEY) [63] and poor recognition of unusual uses for objects (e.g., using a NEWSPAPER to SWAT A FLY) [57], yet they are relatively good at retrieving dominant word meanings and object uses. As noted above, SA patients show symptoms of ideational apraxia in tests of naturalistic action – they struggle to organise their behaviour in tasks such as packing a child's lunchbox, and include irrelevant objects, omit critical objects and/or repeat actions unnecessarily [4, 56]. Together these studies show that infarcts in semantic control regions disrupt a wide range of tasks, both verbal and non-verbal, that involve identifying and categorising items as well as understanding thematic relations.

Given that picture naming errors provided some of the first evidence in favour of the Dual Hub theory [11], it is interesting to note that SD and SA patients also produce different kinds of naming errors: patients with SD produce high-frequency co-ordinate responses (CAMEL → HORSE) and superordinate errors (CAMEL → ANIMAL), while those with SA sometimes produce low frequency object names (CAMEL → ZEBRA) and thematic associations (CAMEL → PYRAMIDS), which rely on knowledge that is largely not retained in SD [64]. The CSC framework offers a different account of why patients with damage to ATL vs. left temporoparietal cortex (along with IFG) make taxonomic and thematic errors respectively. By this view, picture naming errors in SD patients reflect degradation of conceptual knowledge, while errors in SA reflect difficulty constraining retrieval to suit the demands of the task (as opposed to damage to taxonomic and thematic hubs respectively).

The co-ordinate and superordinate responses occur in SD because these patients retain general information better than the differentiating features of specific concepts. In contrast, associative and co-ordinate errors in SA may reflect difficulty selecting an appropriate response among competing alternatives [30, 64].

Although patients with SA have large left-hemisphere lesions, and thus are not well-suited to establishing the brain regions that support semantic control with high spatial precision, brain stimulation studies of healthy participants provide convergent evidence of a necessary role for both left prefrontal and posterior temporal cortex in semantic control. Inhibitory TMS applied to left IFG and pMTG in healthy participants has been shown to disrupt retrieval to an equal degree when control demands are high [71]. In contrast, inhibitory stimulation to semantic control sites does not affect semantic tasks with low control demands or demanding non-semantic judgements [71, 72]. Recent studies have also shown that lesions to left IFG (in patients with SA) and inhibitory TMS to IFG in healthy participants elicits compensatory increases in activation in pMTG, in line with the view that these sites form a functional network [73, 74]. The semantic control sites in left pMTG and IFG also show overlapping patterns of intrinsic connectivity: even in the absence of an overt task, their BOLD responses are highly-correlated across time [12, 72]. These sites tend to be anti-correlated with DMN regions, and they show distinct intrinsic connectivity profiles from AG and ATL [72]. In summary, semantic tasks activate regions of cortex that extend into the DMN, including AG and parts of ATL, but they also activate semantic control sites, which lie within different large-scale networks (see Figure 2).

The evidence, taken together, shows a clear functional dissociation between pMTG and AG. These observations are consistent with the CSC framework but are not adequately explained by the Dual Hub perspective. In some of our recent studies, we have examined the contribution of pMTG and AG to identity matching and thematic association matching, and considered (i) whether one or both of these sites show the hallmarks of a thematic hub, and also (ii) whether these sites are implicated in controlled vs. more automatic patterns of semantic retrieval. In one study, we applied inhibitory TMS to pMTG and AG in healthy participants [72]. TMS disrupted word-picture matching on the basis of both item identity and thematic associations (contrary to the expectations of the Dual Hub account). However, it also produced a double dissociation with respect to the effect of associative strength. TMS to pMTG elicited the greatest disruption to weak association trials, replicating our earlier results [71] and supporting the view that this site makes a critical contribution to semantic control. In contrast, TMS to AG particularly disrupted the efficient retrieval of strong associations [72]. Our recent MEG results are consistent with this functional distinction within temporoparietal cortex [39, 40]. pMTG showed a more substantial oscillatory response in weak association trials,

while AG (along with ATL) showed a larger response to pairs of words that were linked by a strong association. These findings suggest that AG and ATL guide the efficient retrieval of strong associations that are well-supported by representations in the long-term conceptual store (see above). In contrast, when the structure of long-term knowledge cannot readily produce the pattern of retrieval required by the task, semantic control regions including pMTG appear to be recruited more strongly.

Semantic control regions including left IFG and pMTG appear to be distinct from, yet partially overlapping with, multiple-demand regions implicated in executive control across domains – in regions such as inferior frontal sulcus and lateral occipital cortex [12, 60]. Multiple-demand regions that support executive control are likely to be recruited in order to maintain and implement the overarching goal (e.g., task instructions) in semantic tasks. However, in the situations tapping semantic control outlined above, which involve matching RACING CAR with CHAMPAGNE (thematic match) and MEERKAT with CLOWN FISH (taxonomic match), the exact basis of the match cannot be fully specified by the task instructions, and instead the basis of the link has to come from semantic memory itself. We have suggested that, in these circumstances, direct interaction between domain-general executive brain regions and conceptual representations in ATL may be insufficient for efficient semantic retrieval, since patterns of semantic similarity have to reflect non-dominant characteristics of concepts which are only weakly instantiated in long-term memory [12]. Semantic control regions might provide a mechanism by which adaptive coding of rapidly-changing goals can be integrated with long-term knowledge to provide a representation of aspects of knowledge that are currently required for the task or context [12]. These semantic control regions have strong intrinsic and structural connectivity with both the ATL semantic hub and domain-general executive control – architecture which is consistent with this integrative account. In line with this proposal, Dixon et al. recently demonstrated a variant of the frontoparietal control network which has relatively strong connectivity with DMN, and which is implicated in semantic processing. Interestingly, this control network variant was also implicated in action processing in a neuroimaging meta-analysis [75], in line with our previous observation that contrasts focussed on semantic control and action feature matching overlap within a single fMRI study [5].

How can we understand functional dissociations within the semantic network?

The review of studies above provides evidence that left pMTG supports semantic control (along with other regions such as IFG), but there is also compelling research showing that pMTG supports action understanding [46, 47] and tool recognition [48] and shows a stronger response to verbs than nouns

[49-51], consistent with the response profile expected for a thematic hub. In recent studies, we have considered whether these ideas are related [5, 76]. One possibility is that judgements involving verbs (relative to nouns) and actions (relative to objects) often have higher control demands, and/or a stronger need to shape conceptual retrieval to suit the context. This could be the basis for meta-analytic results that highlight pMTG as critical for action, tool and event semantic tasks although further research is needed to test this proposal.

In one study [5], we tested the effects of two distinct manipulations on the BOLD response within pMTG and other semantic control regions. First, we contrasted hard feature matching judgements and easy global semantic judgements to manipulate semantic control demands; secondly, we contrasted judgements about action features with judgements about non-action (colour) features. We found that these contrasts produced overlapping clusters in IFG, pMTG and preSMA – in other words, across much of the semantic control network. In a second study [76], we found that patients with SA (who have semantic control deficits) and healthy participants under dual task conditions (eliciting depleted control resources) showed greater difficulty on the retrieval of weak thematic relations, which require semantic control to identify a linking context, relative to strong thematic relations and identity matching for general and specific concepts. These findings support the view that the semantic control network might make an important contribution to event understanding by allowing the flexible retrieval of knowledge in a way that reflects the requirements of the context. These manipulations of control capacity did not interact with specificity in identity matching, even though specific objects are harder to identify. This last observation shows that semantic control demands are not the only factor contributing to task difficulty in semantic cognition.

Many aspects of this account remain speculative. While the networks implicated in semantic control and action/event understanding largely overlap, some responses within pMTG cannot be readily accounted for in terms of semantic control demands. For example, temporal-occipital cortex proximal to semantic control regions in pMTG code for actions at relatively abstract levels (e.g. open/close bottle relates to open/close box) [77] – and it is not clear how these responses can be directly related to semantic control demands. Moreover, we and others have observed stronger responses in pMTG to thematic vs. taxonomic decisions [40], or to verb vs. noun processing [54], even in the absence of a task difficulty difference between conditions. There are several ways in which the responses in pMTG to semantic control demands and action/event/thematic processing can be reconciled. One possibility is that there are multiple functional subdivisions within pMTG, and adjacent yet distinct regions support different aspects of semantic cognition. In line with this proposal, Peelen et al. found an action-specific site that was posterior and yet close to the verb-processing peak within pMTG [49]. Alternatively, manipulations of semantic control and judgements

of thematic or event relations might rely on shared computational principles, explaining the similarity of large-scale networks (beyond pMTG) that are implicated in these aspects of cognition [5, 53]. We have suggested that pMTG might provide a dynamically-updated conceptual 'context' which supports the tailored retrieval of currently-relevant knowledge, even when this information is not the most strongly encoded within long-term memory [39]. This type of conceptual context would be expected to play a crucial role in the recovery of weakly-instantiated knowledge that is important to the ongoing circumstances, but a less crucial role for dominant features or associations which are thought to be readily recovered within ATL without additional processing. However, semantic tasks involving thematic links and verbs might be more reliant on conceptual context than difficulty-matched tasks involving taxonomic links and nouns. Future research should investigate the emergence of contextually-guided semantic cognition, both along the cortical surface (in order to explore the relevance of known functional subdivisions in pMTG) and through time (as representations of currently-relevant aspects of meaning interact with control processes to drive ongoing semantic retrieval in a tailored fashion).

In conclusion, semantic control may support our ability to shape retrieval to suit the circumstances – across both taxonomic and thematic trials. However, this requirement might typically be taxed more heavily by thematic judgements than identity matching tasks, by verb more than noun processing, and by event more than object-focussed tasks. As noted by Lambon Ralph et al. (2016), we use the same knife when making a sandwich to spread butter, cut cheese and scoop chutney – thus the meaning of this object within a task can change according to the exact temporo-spatial context. The meaning of concepts in tasks and conversations in everyday life varies in a similar way, highlighting the common processes involved in semantic control and event understanding. These common processes may explain why semantic control and action/event understanding recruit overlapping neural networks and why patients with semantic aphasia have difficulty controlling semantic retrieval across diverse types of semantic tasks, while showing the symptoms of ideational apraxia.

1. Lambon Ralph, M.A., et al., *The neural and computational bases of semantic cognition.* Nature Reviews Neuroscience, 2017. **18**(1): p. 42.
2. Yee, E. and S.L. Thompson-Schill, *Putting concepts into context.* Psychon Bull Rev 2016. **23**: p. 1015-1027.
3. Krieger-Redwood, K., et al., *Conceptual control across modalities: Graded specialisation for pictures and words in inferior frontal and posterior temporal cortex.* Neuropsychologia, 2015. **76**: p. 92-107.
4. Corbett, F., et al., *Different impairments of semantic cognition in semantic dementia and semantic aphasia: evidence from the non-verbal domain.* Brain, 2009. **132**(9): p. 2593-2608.
5. Davey, J., et al., *Shared neural processes support semantic control and action understanding.* Brain and Language, 2015. **142**: p. 24-35.

6. Mirman, D., J.F. Landrigan, and A.E. Britt, *Taxonomic and thematic semantic systems.* Psychol Bull, 2017. **143**(5): p. 499-520.
7. Binder, J.R. and R.H. Desai, *The Neurobiology of Semantic Memory.* Trends Cogn Sci, 2011. **15**(11): p. 527-36.
8. Reilly, J., et al., *Linking somatic and symbolic representation in semantic memory: the dynamic multilevel reactivation framework.* Psychonomic bulletin & review, 2016. **23**(4): p. 1002-1014.
9. Patterson, K., P.J. Nestor, and T.T. Rogers, *Where do you know what you know? The representation of semantic knowledge in the human brain.* Nat Rev Neurosci, 2007. **8**(12): p. 976-87.
10. Pulvermüller, F., *How neurons make meaning: brain mechanisms for embodied and abstract-symbolic semantics.* Trends in Cognitive Sciences, 2013. **17**(9): p. 458-470.
11. Schwartz, M.F., et al., *Neuroanatomical dissociation for taxonomic and thematic knowledge in the human brain.* Proc Natl Acad Sci U S A, 2011. **108**(20): p. 8520-4.
12. Davey, J., et al., *Exploring the role of the posterior middle temporal gyrus in semantic cognition: Integration of anterior temporal lobe with executive processes.* NeuroImage, 2016. **137**: p. 165-177.
13. Badre, D., et al., *Dissociable Controlled Retrieval and Generalized Selection Mechanisms in Ventrolateral Prefrontal Cortex.* Neuron, 2005. **47**(6): p. 907-918.
14. Hoffman, P., J.L. McClelland, and M.A. Lambon Ralph, *Concepts, control and context: A connectionist account of normal and disordered semantic cognition.* Psychological Review, 2018. **125**(3): p. 293-328.
15. Jefferies, E., *The neural basis of semantic cognition: Converging evidence from neuropsychology, neuroimaging and TMS.* Cortex, 2013. **49**(3): p. 611-625.
16. Mahon, B.Z. and A. Caramazza, *What drives the organization of object knowledge in the brain?* Trends Cogn Sci, 2011. **15**(3): p. 97-103.
17. Yarkoni, T., et al., *Large-scale automated synthesis of human functional neuroimaging data.* Nature methods, 2011. **8**(8): p. 665-670.
18. Chiou, R., et al., *Controlled semantic cognition relies upon dynamic and flexible interactions between the executive 'semantic control' and hub-and-spoke 'semantic representation' systems.* Cortex, 2018. **103**: p. 100-116.
19. Visser, M., et al., *Both the middle temporal gyrus and the ventral anterior temporal area are crucial for multimodal semantic processing: distortion-corrected fMRI evidence for a double gradient of information convergence in the temporal lobes.* J Cogn Neurosci, 2012. **24**(8): p. 1766-78.
20. Clarke, A., K.I. Taylor, and L.K. Tyler, *The evolution of meaning: spatio-temporal dynamics of visual object recognition.* J Cogn Neurosci, 2011. **23**(8): p. 1887-99.
21. Mollo, G., et al., *Oscillatory dynamics supporting semantic cognition: MEG evidence for the contribution of the anterior temporal lobe hub and modality-specific spokes.* PLoS ONE, 2017. **12**(1).
22. Tsagkaridis, K., et al., *The role of action representations in thematic object relations.* Front Hum Neurosci, 2014. **8**: p. 140.
23. Clarke, A., et al., *From Perception to Conception: How Meaningful Objects Are Processed over Time.* Cerebral Cortex, 2013. **23**(1): p. 187-197.
24. Hodges, J.R. and K. Patterson, *Semantic dementia: a unique clinicopathological syndrome.* Lancet Neurol, 2007. **6**(11): p. 1004-14.
25. Bozeat, S., et al., *Non-verbal semantic impairment in semantic dementia.* Neuropsychologia, 2000. **38**(9): p. 1207-15.
26. Pobric, G., E. Jefferies, and M.A. Lambon Ralph, *Amodal semantic representations depend on both anterior temporal lobes: Evidence from repetitive transcranial magnetic stimulation.* Neuropsychologia, 2010. **48**(5): p. 1336-1342.

27. Pobric, G., E. Jefferies, and M.A. Lambon Ralph, *Category-Specific versus Category-General Semantic Impairment Induced by Transcranial Magnetic Stimulation.* Current Biology, 2010. **20**(10): p. 964-968.
28. Jackson, R.L., et al., *The Nature and Neural Correlates of Semantic Association versus Conceptual Similarity.* Cerebral Cortex, 2015. **25**(11): p. 4319-4333.
29. Jefferies, E., et al., *Comprehension of concrete and abstract words in semantic dementia.* Neuropsychology, 2009. **23**(4): p. 492-499.
30. Rogers, T.T., et al., *Disorders of representation and control in semantic cognition: Effects of familiarity, typicality, and specificity.* Neuropsychologia, 2015. **76**: p. 220-239.
31. Lambon Ralph, M.A., et al., *Naming in semantic dementia--what matters?* Neuropsychologia, 1998. **36**(8): p. 775-784.
32. Snowden, J.S. and D. Neary, *Relearning of verbal labels in semantic dementia.* Neuropsychologia, 2002. **40**(10): p. 1715-1728.
33. Jefferies, E., T.T. Rogers, and M.A.L. Ralph, *Premorbid expertise produces category-specific impairment in a domain-general semantic disorder.* Neuropsychologia, 2011. **49**(12): p. 3213-3223.
34. Merck, C., et al., *When the zebra loses its stripes but is still in the savannah: Results from a semantic priming paradigm in semantic dementia.* Neuropsychologia, 2014. **53**: p. 221-232.
35. Bemis, D.K. and L. Pylkkänen, *Basic linguistic composition recruits the left anterior temporal lobe and left angular gyrus during both listening and reading.* Cerebral Cortex, 2013. **23**(8): p. 1859-1873.
36. Poortman, E.B. and L. Pylkkänen, *Adjective conjunction as a window into the LATL's contribution to conceptual combination.* Brain and Language, 2016. **160**: p. 50-60.
37. Price, A.R., et al., *Converging Evidence for the Neuroanatomic Basis of Combinatorial Semantics in the Angular Gyrus.* The Journal of Neuroscience, 2015. **35**(7): p. 3276.
38. Pallier, C., A.-D. Devauchelle, and S. Dehaene, *Cortical representation of the constituent structure of sentences.* Proceedings of the National Academy of Sciences, 2011. **108**(6): p. 2522-2527.
39. Teige, C., et al., *Dynamic semantic cognition: Characterising coherent and controlled conceptual retrieval through time using magnetoencephalography and chronometric transcranial magnetic stimulation.* Cortex, 2018. **103**: p. 329-349.
40. Teige, C., et al., *Temporal lobe dissociations in semantic cognition: Oscillatory evidence for a process account of thematic and taxonomic differences.* submitted.
41. van Ackeren, M.J., et al., *Oscillatory neuronal activity reflects lexical-semantic feature integration within and across sensory modalities in distributed cortical networks.* Journal of Neuroscience, 2014. **34**(43): p. 14318-14323.
42. Mirman, D. and K.M. Graziano, *Damage to temporo-parietal cortex decreases incidental activation of thematic relations during spoken word comprehension.* Neuropsychologia, 2012. **50**(8): p. 1990-1997.
43. Tsagkaridis, K., et al., *The role of action representations in thematic object relations.* Frontiers in Human Neuroscience, 2014. **8**(140): p. 1-12.
44. Kalénine, S. and L.J. Buxbaum, *Thematic knowledge, artifact concepts, and the left posterior temporal lobe: Where action and object semantics converge. .* Cortex, 2016. **82**: p. 164-178.
45. Wurm, M. and A. Caramazza, *Representation of action concepts in left posterior temporal cortex that generalize across vision and language.* bioRxiv, 2018: p. 361220.
46. Caspers, S., et al., *ALE meta-analysis of action observation and imitation in the human brain.* NeuroImage, 2010. **50**(3): p. 1148-1167.
47. Urgesi, C., M. Candidi, and A. Avenanti, *Neuroanatomical substrates of action perception and understanding: an anatomic likelihood estimation meta-analysis of lesion-symptom mapping studies in brain injured patients.* Frontiers in human neuroscience, 2014. **8**: p. 344-344.

48. Ishibashi, R., et al., *The neural network for tool-related cognition: An activation likelihood estimation meta-analysis of 70 neuroimaging contrasts.* Cognitive Neuropsychology, 2016. **33**(3-4): p. 241-256.
49. Peelen, M.V., D. Romagno, and A. Caramazza, *Independent Representations of Verbs and Actions in Left Lateral Temporal Cortex.* Journal of Cognitive Neuroscience, 2012. **24**(10): p. 2096-2107.
50. Bedny, M., et al., *Concepts Are More than Percepts: The Case of Action Verbs.* The Journal of Neuroscience, 2008. **28**(44): p. 11347.
51. Horoufchin, H., et al., *Action and object words are differentially anchored in the sensory motor system - A perspective on cognitive embodiment.* Scientific Reports, 2018. **8**(1): p. 6583.
52. Bedny, M., S. Dravida, and R. Saxe, *Shindigs, brunches, and rodeos: the neural basis of event words.* Cogn Affect Behav Neurosci, 2014. **14**(3): p. 891-901.
53. Mollo, G., et al., *Context-dependent lexical ambiguity resolution: MEG evidence for the time-course of activity in left inferior frontal gyrus and posterior middle temporal gyrus.* Brain and Language, 2018. **177-178**: p. 23-36.
54. Papeo, L., et al., *The origin of word-related motor activity.* Cerebral cortex (New York, N.Y. : 1991), 2015. **25**(6): p. 1668-1675.
55. Papeo, L. and A. Lingnau, *First-person and third-person verbs in visual motion-perception regions.* Brain and Language, 2015. **141**: p. 135-141.
56. Corbett, F., E. Jefferies, and M.A. Lambon Ralph, *Exploring multimodal semantic control impairments in semantic aphasia: Evidence from naturalistic object use.* Neuropsychologia, 2009. **47**(13): p. 2721-2731.
57. Corbett, F., E. Jefferies, and M.A. Lambon Ralph, *Deregulated Semantic Cognition Follows Prefrontal and Temporo-parietal Damage: Evidence from the Impact of Task Constraint on Nonverbal Object Use.* Journal of Cognitive Neuroscience, 2010. **23**(5): p. 1125-1135.
58. Kalenine, S., et al., *The sensory-motor specificity of taxonomic and thematic conceptual relations: a behavioral and fMRI study.* Neuroimage, 2009. **44**(3): p. 1152-62.
59. Raichle, M.E., et al., *A default mode of brain function.* Proceedings of the National Academy of Sciences, 2001. **98**(2): p. 676.
60. Noonan, K.A., et al., *Going beyond inferior prefrontal involvement in semantic control: evidence for the additional contribution of dorsal angular gyrus and posterior middle temporal cortex.* J Cogn Neurosci, 2013. **25**(11): p. 1824-50.
61. Humphreys, G.F. and M.A. Lambon Ralph, *Fusion and Fission of Cognitive Functions in the Human Parietal Cortex.* Cereb Cortex, 2015. **25**(10): p. 3547-60.
62. Yeo, B.T., et al., *The organization of the human cerebral cortex estimated by intrinsic functional connectivity.* J Neurophysiol, 2011. **106**(3): p. 1125-65.
63. Noonan, K.A., et al., *Elucidating the Nature of Deregulated Semantic Cognition in Semantic Aphasia: Evidence for the Roles of Prefrontal and Temporo-parietal Cortices.* Journal of Cognitive Neuroscience, 2009. **22**(7): p. 1597-1613.
64. Jefferies, E. and M.A. Lambon Ralph, *Semantic impairment in stroke aphasia versus semantic dementia: a case-series comparison.* Brain, 2006. **129**(8): p. 2132-2147.
65. Jefferies, E., K. Patterson, and M.A.L. Ralph, *Deficits of knowledge versus executive control in semantic cognition: Insights from cued naming.* Neuropsychologia, 2008. **46**(2): p. 649-658.
66. Gardner, H.E., et al., *The Differential Contributions of pFC and Temporo-parietal Cortex to Multimodal Semantic Control: Exploring Refractory Effects in Semantic Aphasia.* Journal of Cognitive Neuroscience, 2012. **24**(4): p. 778-793.
67. Thompson, H.E., et al., *Varieties of semantic 'access' deficit in Wernicke's aphasia and semantic aphasia.* Brain, 2015. **138**(Pt 12): p. 3776-92.
68. Jefferies, E., et al., *Refractory effects in stroke aphasia: A consequence of poor semantic control.* Neuropsychologia, 2007. **45**(5): p. 1065-1079.

69. Warrington, E.K. and L. Cipolotti, *Word comprehension. The distinction between refractory and storage impairments.* Brain, 1996. **119 (Pt 2)**: p. 611-25.
70. Mirman, D. and A.E. Britt, *What we talk about when we talk about access deficits.* Philos Trans R Soc Lond B Biol Sci, 2014. **369**(1634): p. 20120388.
71. Whitney, C., et al., *The neural organization of semantic control: TMS evidence for a distributed network in left inferior frontal and posterior middle temporal gyrus.* Cereb Cortex, 2011. **21**(5): p. 1066-75.
72. Davey, J., et al., *Automatic and Controlled Semantic Retrieval: TMS Reveals Distinct Contributions of Posterior Middle Temporal Gyrus and Angular Gyrus.* Journal of Neuroscience, 2015.
73. Hallam, G.P., et al., *Charting the effects of TMS with fMRI: Modulation of cortical recruitment within the distributed network supporting semantic control.* Neuropsychologia, 2016. **93**: p. 40-52.
74. Hallam, G.P., et al., *Task-based and resting-state fMRI reveal compensatory network changes following damage to left inferior frontal gyrus.* Cortex, 2018. **99**: p. 150-165.
75. Dixon, M.L., et al., *Heterogeneity within the frontoparietal control network and its relationship to the default and dorsal attention networks.* Proceedings of the National Academy of Sciences, 2018. **115**(7): p. E1598.
76. Thompson, H., et al., *Semantic control deficits impair understanding of thematic relationships more than object identity.* Neuropsychologia, 2017. **104**: p. 113-125.
77. Wurm, M.F. and A. Lingnau, *Decoding Actions at Different Levels of Abstraction.* The Journal of Neuroscience, 2015. **35**(20): p. 7727.